Polypore assemblages in boreal old-growth forests, and associated Coleoptera

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Contents

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Schigel, D.S. 2009: Polypore assemblages in boreal old-growth forests, and associated Coleoptera. — Publications in Botany from the University of Helsinki, 44 pp.

This thesis is based on the following publications:

I Schigel, D.S., Niemelä, T., Similä, M., Kinnunen, J. & Manninen, O. 2004: Polypores and associated beetles of the North Karelian Biosphere Reserve, eastern Finland. — *Karstenia* 44: 35–56.

II Schigel, D.S. & Toresson, H.G. 2005: New records of Polyporus pseudobetulinus, a rare polypore fungus (Basidiomycota, Aphyllophorales) in Scandinavia, and notes on associated beetles. — *Memoranda Societatis pro Fauna et Flora Fennica* 81: 102–107.

III Schigel, D.S., Niemelä, T. & Kinnunen J. 2006: Polypores and associated beetles of western Finnish Lapland. — *Karstenia* 46: 37–64.

IV Schigel, D.S. 2007: Fleshy fungi of the genera *Armillaria*, *Pleurotus*, and *Grifola* as habitats of Coleoptera. — *Karstenia* 47: 37–48.

V Schigel, D.S. 2009: Polypore assemblages in boreal old-growth forests, and notes on associated beetles in Finland, manuscript.

These studies are referred to in the text by their Roman numerals.

The following table indicates the major contributions of authors to the original articles or manuscripts.

Paper	I	II	III	IV	V
Idea of the study	DSS, TN	DSS, TN	DSS, TN	DSS, TN	DSS
Material collection and identification	DSS, TN, JK, MS, OM	DSS, TN, HGT	DSS, TN, JK	DSS	DSS, TN, JK
Ideas and processing of analyses	DSS, TN	DSS, HGT	DSS, TN	DSS, TN	DSS, TN
Manuscript preparation	DSS	DSS	DSS	DSS	DSS

JK = Juha Kinnunen, OM = Olli Manninen, TN = Tuomo Niemelä, MS = Maarit Similä, HGT = Hans-Göran Toresson. Other contributors are acknowledged in the individual studies.

Abstract

Schigel, D.S. 2009: Polypore assemblages in boreal old-growth forests, and associated Coleoptera. — Publications in Botany from the University of Helsinki, 44 pp.

This thesis examines assemblages of wood-decaying fungi in Finnish old-growth forests, and patterns of species interactions between fruit bodies of wood-rotting Basidiomycetes and associated Coleoptera. The present work is a summary of four original publications and a manuscript, which are based on empirical observations and deal with the prevalence of polypores in old-growth forests, and fungicolous Coleoptera. The study area consists of eleven old-growth, mostly spruce- and pine-dominated, protected forests rich in dead wood in northern and southeastern Finland. Supplementary data on fungus–beetle interactions were collected in southern Finland and the Åland Islands. 11251 observations of fruit bodies from 153 polypore species were made in 789 forest compartments. Almost a half of the polypore species demonstrated a distinct northern or southeastern trend of prevalence. Polypores with a northern prevalence profile were in extreme cases totally absent from the Southeast, although almost uniformly present in the North. These were *Onnia leporina*, *Climacocystis borealis*, *Antrodiella pallasii*, *Skeletocutis chrysella*, *Oligoporus parvus, Skeletocutis lilacina*, and *Junghuhnia collabens*. Species with higher prevalence in the southeastern sites were *Bjerkandera adusta*, *Inonotus radiatus, Trichaptum pargamenum*, *Antrodia macra*, and *Phellinus punctatus*.

198 (86%) species of Finnish polypores were examined for associated Coleoptera. Adult beetles were collected from polypore basidiocarps in the wild, while their larvae were reared to adulthood in the lab. Spatial and temporal parallels between the properties of polypore fruit body and the species composition of Coleoptera in fungus–beetle interactions were discussed. New data on the biology of individual species of fungivorous Coleoptera were collected. 116 species (50% of Finnish polypore mycota) were found to host adults and/or larvae of 179 species from 20 Coleoptera families. Many new fungus–beetle interactions were found among the 614 species pairs; these included 491 polypore fruit body – adult Coleoptera species co-occurrences, and 122 fruit body – larva interrelations. 82 (41%) polypore species were neither visited nor colonized by Coleoptera. The total number of polyporicolous beetles in Finland is expected to reach 300 species.

Key words: Basidiomycetes, fruit body, prevalence, fungivory, dead wood.

Introduction

Decaying wood is a unique, spatially and temporally discrete terrestrial habitat where Animalia, Plantae, Fungi, Protista, and Prokaryota co-occur and interact. The role of dead wood in forest ecosystems has been a hot research topic in the Nordic countries and beyond (see Review of Literature below). Autotrophic producers, and woody plants in particular, support a high diversity of consumers and decomposers representing several trophic levels and specializations.

Fungi are among the most widespread wood decayers, equipped with enzymes efficient in cellulolysis and lignin degradation. Consequently, organic substances of plants turn into fungal mycelia and fruit bodies, which make for an attractive food source for many organisms. Dead wood is a central element of complex and species-rich food webs, which include organisms dependent on wood, such as fungi and wood-boring insects, as well as their parasitoids, predators (Johansson et al. 2007) and fungivores. The presence of fungal mycelia affects the species composition of saproxylic beetles attracted by dead wood (Johansson et al. 2006, Olsson 2008).

In Finland polypores are arguably one of the best-studied groups of forest organisms from the taxonomical point of view (Niemelä 2005). Their importance for nature conservation and forest management (Penttilä 2004, Hottola & Siitonen 2008) became widely acknowledged after the ecological preferences of individual species were documented in detail (Renvall 1995). The patterns of occurrence and distribution of wood-decaying fungi reflect their dispersal abilities (Komonen 2005) and habitat preferences. Some species serve as indicators of old-growth forests rich in dead wood (Kotiranta & Niemelä 1996, Niemelä et al. 2005, Halme et al. 2008), and many are red-listed (Rassi et al. 2001). A national overview of the distribution of Aphyllophoroid fungi by vegetation zones (Kotiranta et al. 2009) was recently published, summarizing significant collecting and research activity of both professionals and amateurs.

Human activities threaten fungi that depend on dead wood (Penttilä 2004, Junninen 2007). Rare and poorly-known species (Kotiranta & Niemelä 1996, Rassi et al. 2001) are among the most vulnerable elements of the natural ecosystems, and they are at risk of decline or extinction. For many of such species ecological preferences and factors critical for survival are insufficiently documented (Sverdrup-Thygeson & Midtgaard 1998). As a result, poorly known species may vanish from their habitats due to the lack of species-specific information even if advanced nature conservation practices are applied. Junninen and collaborators (2006) explored the gradients of succession and naturalness in boreal pine-dominated forests. They concluded that a network of forest reserves and an input of new dead wood there are essential to preserve the mycota of wood decayers, and call for better forestry practices.

Fungal fruit bodies make variable and compact habitats for insect fungivores. This variability is high both temporally and spatially: the speed of growth and decomposition, predictability and yearly fluctuations in fructification, durational stability of fruit bodies, and their phenology – all these vary (Ryvarden 1991). Small numbers of available fruit bodies, or minor differences among them, are contrasted as the quantity *vs.* quality hypotheses of insect polyphagy, an important risk-spreading strategy among fungivores

(Hanski 1989). Similarly to plant–herbivore systems, fungus–fungivore systems are also characterised by grazing pressure, defensive mechanisms and dispersal relations. Fungal mycelia, unlike the fruit bodies, greatly influence the nutritional turnover in an ecosystem. Mycelium is often consumed together with its woody substrate, and so the term *fungivorous* is used in relation to organisms, whose larvae selectively consume fungi. Other old and new terms are explained in the corresponding sections of Studies I–V.

The majority of publications on insect fungivory have focused on fruit bodies, and this thesis is no exception. Fruit bodies of polypores are attractive study objects due to their compactness, host specificity and variable presence. On the contrary, agarics are ephemeral and unpredictable in their fructification, which limits the range of beetle species able to dwell inside.

Four main factors seem to have an effect on the presence, composition and richness of fungivorous beetle species (Økland 1995 and references therein): hyphal structure of a fungus, its hardness, and durational stability, and insect mouthpart adaptations (Betz et al. 2003). Aggregation (and frequency of occurrence) may be used as a measure of habitat preference, caused by a combination of dietary and non-dietary reasons, such as mate location (Jonsell & Nordlander 1995, Jonsson et al. 1997). Fungivorous insects influence the fungal community in a constructive (spore dispersal), but mostly in a destructive way (Shaw 1992, Guevara et al. 2000c).

Fungi attract insects of several orders (Lawrence 1989), Diptera and Coleoptera being the most species-rich. In general, adaptations to moist habitats of Diptera and dry habitats of Coleoptera separate these orders ecologically. Larvae of Diptera are mostly adapted to soft, moist or liquid substrata and are diverse in mushrooms, while larvae of Coleoptera thrive in dry and firm media, and therefore abound in polypores. Invertebrates other than Coleoptera and Diptera cause only minor destruction to polypore fruit bodies. Fungivory in Coleoptera seems to have evolved independently several times (Crowson 1981). Perennial polypores are more stable than annuals which in turn are more stable than mushrooms. The diversity–stability hypothesis may explain patterns of species richness among the specialists in different types of fungal substrates (Hanski 1989).

Interspecific relations between polypores (mainly fruit bodies) and beetles (mainly larvae) have been the focus of many studies. However, ecological paradigms based on verification and statistical analysis typically requires large datasets. At present our knowledge is centred round a few easy-to-recognise fungi and abundant fungivorous beetles (Table 1). Such study settings allowed deep research in particular aspects of beetle fungivory, including beetle behaviour, role of olfactory stimuli, and habitat fragmentation. An overall view with as many polypore species as possible would also be needed in order to complete the picture.

Aims of the study

With my work, I try to approach the first part of the key question of community ecology (McCune & Grace 2002): *who is living with whom*, and why? I aim to describe and compare the polypore assemblages in the least disturbed old-growth forests of the Finnish North and Southeast. These areas may serve as local reference areas with high species diversity of fungi.

Komonen (2003a) and Johansson (2006) call for more data on fungus–insect interactions. The lack and insufficiency of biodiversity data are also seen as “the number one challenge” in applying conservation planning techniques into practice (Arponen 2009). Polypores include many red-listed species and indicator species which are increasingly used in nature conservation in the Nordic countries. In order to qualitatively study the associations between wood-decayers and Coleoptera, species coverage was aimed to include less known host fungi. Most of the energy was invested to collect material directly from the wild.

The specific aims of this thesis are to explore**:**

1) Polypore assemblages in boreal old-growth forests in the Finnish North *vs.* Southeast, and their qualitative differences.
2) Species interactions and natural history of communities and individual species of wood-decaying fungi and their beetles.

2. Review of the literature

Finnish expertise in polypores is high, both in taxonomy and ecology. Studies of polypore assemblages (Halme et al. 2008) have explored various aspects of their ecology, such as temporal dynamics and habitat preferences (Renvall 1995), importance for nature conservation and forest management (Penttilä 2004, Junninen 2007, Hottola & Siitonen 2008), dispersal abilities (Komonen 2005), and response to forest succession and naturalness (Junninen et al. 2006). Many polypores are red-listed (Rassi et al. 2001) or/and indicators of old-growth forests rich in dead wood (Kotiranta & Niemelä 1996, Niemelä et al. 2005, Halme et al. 2008). Polypore distribution by vegetation zones has been recently reviewed (Kotiranta et al. 2009), and comparisons of polypore assemblages along geographical gradients have been published (Väisänen 1992, Siitonen et al. 2001, Gu et al. 2002, Penttilä et al. 2006, Hottola & Siitonen 2008).

Associations between fungi and other organisms have been an attractive study object for mycologists, entomologists and ecologists. Saalas (1917, 1923) and Palm (1951, 1959) were among the first to document saproxylic (including fungivorous) Coleoptera in the Nordic region. High species diversity of beetles on sporulating fruit bodies and the difference in diurnal and nocturnal activities of the Coleoptera were shown (Paviour-Smith 1965, Nilsson 1997, Hågvar 1999).

Difficulties in collecting, rearing, and, in particular, identification of polypores and fungivorous beetles have restricted many studies to certain widespread or conspicuous fungi, e.g. *Polyporus squamosus* (Klimaszewski & Peck 1987), *Ganoderma applanatum* (Tuno 1999), or beetles, e.g. *Bolitophagus reticulatus* (Knutsen et al. 2000, Sverdrup-Thygeson & Midtgaard 1998) and *Bolithotherus cornutus* (Connor 1988, 1989, Kehler & Bondrup-Nielsen 1999). Dead wood and saproxylic organisms are in the focus of a number of mostly Nordic studies (Speight 1989, Thunes 1993, Midtgaard 1996, Jonsell 1999, Jonsson 2002, Martikainen 2000, Rukke 2000a, Sverdrup-Thygeson 2000, Jonsson & Kruys 2001, Kruys 2001, Stokland 2001, Similä 2002, Heilmann-Clausen & Christensen 2003, Komonen 2003a, Penttilä 2004, Johansson 2006, Olsson 2008).

Dead wood is an important but dwindling element of European forests. Hundreds of publications explore various sides of this ecological theme, of which several tens explore insect fungivory (Table 1, and refs. in Jonsell 1999, Komonen 2003a). Fogel (1975) provides earlier references on the topic. Schlaghamerský (2000) studied beetles (including fungivores) and ants of hardwood floodplain forests of the Czech Republic. He focused mainly on insect associations with different types of dead wood in various biotopes using traps. Martikainen and Kaila (2004) compare different methods of sampling saproxylic beetles. Martikainen and Kouki (2003) argue that representative samples in the surveys of threatened and near-threatened beetles should exceed 200, optimally 400 species, and demonstrate a need for methodological shortcuts, such as indicator species, in order to avoid collecting and identifying hundreds of thousands of specimens. For fungicolous beetles direct collecting on the host and rearing larvae into adults are essential for describing habitat requirements of individual taxa.

For a broader overview of insect fungivory see Wheeler & Blackwell (1984), Koch (1989a, b), and Wilding et al. (1989). Blackwell (1984) reviewed beetle relations with myxomycetes, Gilbertson (1984) with wood-rotting Basidiomycetes, and Bruns (1984) with boletes. Ashe (1984) studied fungus–beetle interactions of Aleocharinae *vs.* mushrooms, and Crowson (1984) of Coleoptera *vs.* Ascomycetes. Staphylinidae, Phalacridae, and Leiodidae *vs.* fungi were reviewed by Newton (1984), Steiner (1984), and Wheeler (1984), respectively. To limit repetitive references to these well-known classical works, below I highlight less known literature sources.

Cyrillic literature remains difficult to access and interpret for the majority of western readers. Partial information blockade of the former Soviet Union from the global scientific community prevented the development of advanced research, and this delay may still be seen. The isolation, however, had also a positive effect in kicking off large-scale collecting of species-specific information in a vast area from European Russia, Belarus and Ukraine to the Urals, Western Siberia and the Russian Far East (Logvinovsky 1980, 1985, Yuferev 1982, Kompantsev 1982, 1984, 1988, Kompantsev & Potockaya 1987, Kompantseva 1987a–c, Krasutsky 1990–1997, Nadvornaya & Nadvorniy 1991, Nikitsky 1993, Nikitsky & Kompantsev 1995, 1997, Nikitsky et al. 1996, 1998, Nikitsky & Tatarinova 2002, Nikitsky & Schigel 2004). More reports were published in small numbers of copies in poorly-distributed scientific journals in Russian. The majority of studies in the former Union focused on certain arthropod taxa (Zaitsev 1982, 1984, Zhantiev 2001), including Latridiidae (Saluk 1989, 1991, 1995), Diptera (Mamaev 1972, 1977, Halidov 1975, 1984, Krivosheina et al. 1986, Zaitsev & Kompantsev 1987, Krivosheina 1991, Jakovlev 1994, Zaitsev 1994), Lepidoptera (Zagulyaev 1973a, b) and Acarina (Makarova 2004).

Even though beetle faunas and polypore mycotas in Europe are reasonably well known, I am not aware of any recent checklists of fungus–beetle interactions which would cover a country or a vegetation zone. Certain beetle taxa and their links to fungi were, however, extensively treated at the regional level, in particular Ciids in southwestern Germany (Reibnitz 1999) and in Sweden (Östergötland to Västerbotten, Jonsell & Nordlander 2004). Atty (1983) reports many fungal hosts for Coleoptera of Gloucestershire, UK, and Orledge & Ewing (2006) provide a detailed review of fungal hosts of *Cis dentatus*. Conrad (1992) report distribution of 16 fungivorous beetles in Germany, and rough distribution maps are available at http://data.gbif.org/species. At a landscape level, Jonsson & Nordlander (2006) report on certain insect species whose colonization rates are affected by distance from an old-growth forest reserve.

There have been a few attempts to draw parallels between the systematic position of beetles (Paviour-Smith 1960a, Lawrence 1973, Kompantsev 1984) or fungi (Jonsell & Nordlander 2004) with the interaction patterns. Certain aspects of fungal chemistry in relation to beetle attraction to fruit bodies (Fäldt et al. 1999) or to the wood penetrated by mycelia of wood-decaying fungi (Johansson et al. 2006) have been explored. One analysis of beetle host-groups (Orledge & Reynolds 2005) combines original and literature data and covers 167 holarctic species of Ciidae; fungal hosts were explored on a genus level.

Books and papers on fungus–beetle interactions published before mid-twentieth century may be more difficult to use for comparisons because of changed taxonomy, and, sometimes, jointly reported data on larvae and adults. Among classical earlier works as those of Weiss (1920), Chagnon (1935), Scheerpeltz & Höffler (1948), Benick (1952), Paviour-Smith (1960–1968b), Pielou & Verma (1968), Matthewman & Pielou (1971), Ackerman & Shenfeldt (1973a–b), Lawrence (1973, 1989), Fogel & Peck (1975), Crowson (1981, 1984), and Newton (1984) should be mentioned. After Benick (1952) studied 1116 species (32004 specimens) of fungicolous beetles in northern Germany, lengthy reports on fungus–beetle links have gone out of fashion in species interaction research and were replaced by more compact ecological studies with strict methodology.

Thunes (1993) tabulates major works on polypore–invertebrate interactions from 1920 to 1989. After 1989, many studies were published in this field, and an update seems to be necessary to place the present study in the context of earlier studies (Table 1). Some major reports and compilations on beetle fungivory were not included in Table 1: Palm (1959), Atty (1983), Nuss (1975), Koch (1989a, b and other *Ökologie* volumes of *Die Käfer Mitteleuropas*), Nikitsky et al. (1996) supply information on fungal hosts of many beetle species in Europe, and of Mycetophagidae from Russia and adjacent countries (Nikitsky 1993). Krasutskiy (2005) provides data on 208 fungicolous beetles and 89 species of host fungi of Urals and Transurals.

Table 1 covers 90 polypore–beetle interaction studies from northern Europe and adjacent countries published after 1950. Even though an effort was made to provide as complete overview as possible, some studies may remain overlooked. 22 polypore–beetle interaction studies were carried out in Sweden, 21 in Norway, 14 in UK, 12 in Finland, 10 in European Russia, 5 in Belarus, 4 in Germany, 3 in Poland, and 1 in Estonia, plus one study covering northern Europe. The main methods in these studies were collecting in the field (44 papers) or rearing (43). Eleven studies were based on trapping, eleven on field experiments, and six on lab experiments. Two studies were based on museum, and one on literature data (Table 1).

This summary table was compiled mainly to overview the species coverage in these studies, and to highlight the need for expanding the taxonomic scope in fungus–beetle interaction research. The size of the species interaction matrix (only polypores × polyporicolous beetles included) was calculated for each study; it should be taken into consideration that usually only a small fraction of such potential fungus–beetle interactions can be realized in nature, and only a fraction of these are observed and reported. Only six studies explored matrices with more than 1 000, and 25 with over 100 potential links (e.g. study system with 10 hosts × 10 consumers). Judging only from the numbers of polypore species and of fungicolous beetles in Finland, it is obvious that possibilities for species of fungi and beetles to come across each other are much broader. The primary task is to identify which of these potential associations are actually real in nature; this question was approached with the present work. Future tasks would be to statistically explore known associations, and to study the ecological processes behind these patterns. Many studies listed in Table 1 and below already explored these questions in depth. Primary research articles on species interactions naturally deal with fewer species than review studies and check lists. Many study systems in Table 1 were based primarily or entirely on conspicuous or widespread fungal and beetle taxa. Thus, *Fomes fomentarius* was a key fungal host in 29 out of 90 studies, *Fomitopsis pinicola* in 23, *Piptoporus betulinus* in 9 studies. Among beetles, *Bolitophagus retuculatus* was in focus of 12 studies (Table 1).

From the 1990s we see a true boom in mostly Nordic studies of species dependent on dead wood (Siitonen, 1994, Bader et al., 1995, Bakke 1999, Martikainen 2001, Alexander 2002) and insect fungivory (Kaila 1993, Thunes 1994, Kaila et al. 1994, 1997, Økland &

Hågvar 1994, Jonsell & Nordlander 1995, 2002, 2004, Yakovlev 1995, Økland 1995, Jonsson et al. 1997, 2001, 2003a, b, Hågvar & Økland 1997, O'Connell & Bogler 1997, Sörensson 1997, Thunes & Willasten 1997, Fossli & Andersen 1998, Rukke & Midtgaard 1998, Sverdrup-Thygeson & Midtgaard 1998, Thunes & Midtgaard 1998, Guevara & Dirzo 1999, Hågvar 1999, Jonsell et al. 1999, 2001, 2003, Andersen et al. 2000, Guevara et al. 2000a–c, Komonen et al., 2000, 2001, 2003, Komonen 2003b, c, Olberg & Andersen 2000, Rukke 2000b, Thunes et al. 2000, Olberg et al. 2001, Siitonen et al. 2001, Yakovlev et al. 2001, Grove 2002, Jørum 2002, Sverdrup-Thygeson & Ims 2002, Jonsson & Jonsell 2003, Komonen & Kouki 2005, Lik 2005, Lik & Barczak 2005, Möller 2005, Selonen, et al. 2005, Dodelin 2006a, b, Jakovlev et al. 2006, Johansson et al. 2006, Jonsson & Nordlander 2006, Polevoi et al. 2006, Stokland et al. 2006, Artéro & Dodelin 2007, Majka 2007).

Insects may affect spore productivity of wood-decaying fungi (Guevara et al. 2000c), but the role of insects as spore vectors has been insufficiently explored. High numbers of spore-attracted beetle species on perennial and/or large fruit bodies of polypores entailed the expectation of mutualistic fungus–beetle relationships (Hågvar 1999). Fossli and Andersen (1998) studied the densities of beetle individuals in fungi, and found that certain fungal genera or species are preferred. They also argue that microclimatic factors, fungal softness and durability are unlikely to explain the host selection. Thunes et al. (2000) found more red-listed species of Coleoptera and more beetle species per unit volume of fruit bodies in areas with high levels of dead wood. Jonsell et al. (2001) found that host size, succession stage, height above the ground and exposure to the sun have an effect on insect species compositions and community structures. The kairomone effect of fungal mycelia in beetle–dead-wood links was studied by Johansson et al. (2007), but fungal spore – adult beetle interactions have been to a large extent unknown.

Experimental studies in insect fungivory demonstrate the role of host and other odours and volatiles in beetle attractions to the polypore fruit bodies. Guevara et al. (2000b) examined four Ciidae beetles attracted by 15 species of fungi in the field (incl. 9 polypores), and experimentally supported the field data that specialist and generalist Ciidae demonstrate different behavioural responses to the odours of three polypore species. Komonen (2008) explored colonization ability of Ciidae associated with *Trametes ochracea*, and proved that ciids may disperse for up to 1.5 km, but demonstrate considerable differences between species.

In Fennoscandian studies beetle communities in *Fomes fomentarius*, *Fomitopsis* spp., *Phellinus* spp., *Ganoderma applanatum*, *Amylocystis lapponica*, *Cerrena unicolor*, *Inonotus obliquus*, *I. radiatus*, *Piptoporus betulinus*, *Pycnoporus cinnabarinus*, *Trametes* spp. and *Trichaptum* spp. have been studied and reported extensively, but beetles of the remaining two hundred species of Nordic polypores were studied seldom, if at all. With the exception of Ehnström & Axelsson (2002) who provide 18 main fungal hosts for 26 polyporicolous beetles, there has been no recent study that documents the interactions of Nordic polypores and their beetles, that takes into account taxonomic novelties, or that investigates as many polypore species as possible. These omissions in the literature provide justification for the present work.

Table 1. Polypore–beetle interaction studies in northern Europe and adjacent countries in 1950–2009. Publications with species-specific information were included; fungi and beetles determined to the genus level were not counted, unless otherwise stated (*). Studies are arranged according to the size of fungus–beetle species interaction matrix (Mx), calculated as N of species of polypores × N of polyporicolous beetle species (NPsp) in the study. Countries are abbreviated to the ISOA3 international codes, Methods (Md) are abbreviated as follows: FC = collecting in the field, FX = field experiments, Lit = based on literature data, LR = rearing in the lab, LX = lab experiments, including genetic studies, Mus = based on museum data, TR = flight-interception traps. Numbers of specimens (N), numbers of species (Nsp), and key taxa in the focus of study are provided for polypores and beetles when possible. Species are abbreviated as follows. **Polypores:** *Alap = Amylocystis lapponica, Ffom = Fomes fomentarius, Fpin = Fomitopsis pinicola, Fros = F. rosea, Gsep = Gloeophyllum sepiarium, Irad = Inonotus radiatus, Irhe = I. rheades, Iobl = I. obliquus, Pbet = Piptoporus betulinus, Pcin = Pycnoporus cinnabarinus, Pign = Phellinus igniarius, Plun = P. lundellii, Pnig = P. nigrolimitatus, Ptre = P. tremulae Psqu = Polyporus squamosus, Toch = Trametes ochracea, Tver = T. versicolor*. **Beetles**: *Bret = Bolitophagus reticulatus, Cbil = Cis bilamellatus, Cbol = C. boleti, Cgla = C. glabratus, Cqua = C. quadridens, Gbol = Gyrophaena boleti, Llun = Lordithon lunulatus, Ohae = Oplocephala haemorrhoidalis, Saff = Sulcacis affinis, Tfun = Tetratoma fungorum.*

				Polypores			Beetles			
Study	**Mx**	**C**	**Md**	**N**	**Nsp**	**Key taxa**	**N**	**Nsp**	**NPsp**	**Key taxa**
Benick 1952	**13130**	DEU	FC, LR	20471	65		32004	1116	202	
Orledge & Reynolds 2005	**9185**	GBR	FC, Lit		55*	*genera		167	167	Ciidae
Nikitsky & Schigel 2004	**5307**	RUS	FC, LR	8765	61			261	87	
Schigel 2002	**4900**	RUS	FC, LR		49			100	100	
Reibnitz 1999	**2160**	DEU	FC, LR		54			40	40	Ciidae
Möller 2005	**1020**	DEU	FC, LR		20			51	51	
Ehnström & Axelsson 2002	**468**	SWE	LR		18			462	26	
Semenov 2007	**468**	RUS	FC		13			238	36	Aleochar-inae
Johansson et al. 2006	**345**	SWE	FC, FX		3	*Fpin, Fros, Pchr*	746	171	115	*Llun*
Tsinkevich 1998	**312**	BLR	FC, LR		13			24	24	Ciidae
Logvinovsky & Holkina 1992	**308**	RUS	FC, LR	173	11	*Ffom*		28	28	
Kompantsev 1984	**288**	RUS	FC, LR		12			24	24	
Tsinkevich 1997b	**240**	BLR	FC, LR	~2000			3374	277	240	
Paviour-Smith 1960a	**221**	GBR	FC, LR	tens	17		tens	16	13	Ciidae
Tsinkevich 1995	**187**	BLR	FC, LR		11			17	17	Ciidae
Økland 1995	**180**	NOR		163	6	*Ptre, Pbet, Fpin, Ffom, Pcin, Irad*		30	30	
Jonsell & Nordlander 2004	**161**	SWE		2265	7			23	23	
Nikitsky & Tatarinova 2002	**155**	RUS	FC, LR		5			19	31	Latridiidae
Olberg & Andersen 2000	**136**	NOR	TR	99	4	*Ffom, Pign, Pnig, Plun.*	7617	178	34	
Tsinkevich 1999	**125**	BLR	FC, LR	100+	1	*Ffom*	1000+	125	125	

				Polypores			Beetles			
Study	**Mx**	**C**	**Md**	**N**	**Nsp**	**Key taxa**	**N**	**Nsp**	**NPsp**	**Key taxa**
Hågvar 1999	**122**	NOR	FC	140	2	*Fpin, Ffom*		61	61	
Thunes 1994	**120**	NOR	FC, LR	338	2	*Fpin Pbet*	2266	60	60	
Fossli & Andersen 1998	**117**	NOR		1000+	9		15500	13	13	Ciidae
Thunes & Willassen 1997	**114**	NOR	LR		2	*Ffom, Pbet*	2266	57	57	
Tsinkevich 1997a	**108**	BLR	FC, LR	350	9		502	12	12	Tenebrio-nidae
Klimaszewski & Peck 1987	**98**	POL	FC		1	*Psqu*	2057	98	98	
Økland 2002	**84**	NOR	TR	690	2	*Fpin, Ffom*		42	42	
Fäldt et al. 1999	**66**	SWE	FX	20	2	*Fpin, Ffom*		33	33	
Selonen et al. 2005	**55**	FIN	LR	1210	55		2164	33		*Gbol, Saff*
Paviour-Smith 1969	**54**	GBR	LR		6		tens	13	9	Ciidae, *Bret*
Ollila 2005	**48**	FIN	FC, LR	104	4	*Antrodia*	138	12	12	Ciidae
Kompantseva 1987c	**40**	RUS	LR		8			5	5	
Jonsell & Nordlander 2002	**38**	SWE	LR	1746	2	*Fpin, Ffom*	~40 000	19	19	
Guevara et al. 2000b	**36**	GBR	FC, LX	227	9			4	4	Ciidae
Jonsell et al. 2001	**32**	SWE	LR	2127	2	*Fpin, Ffom*	~23700	16	16	
Hågvar & Økland 1997	**31**	NOR	TR	30	1	*Fpin*	~12000	46	31	*Gbol*
Siitonen et al. 1996	**30**	FIN, RUS	FC		5	*Trametes, Funalia*		48	6	Ciidae
Økland & Hågvar 1994	**23**	NOR	LR, TR	198	1	*Fpin*		23	23	*Gbol*
Thunes et al. 2000	**17**	NOR	LR	299	1	*Fpin*	12 373	36	17	*Cgla*
Jonsell et al. 1999	**16**	SWE	FX		2	*Fpin, Ffom*		18	8	*Dorcatoma,* Ciidae
Komonen & Kouki 2005	**12**	FIN	LR	351	1	*Toch*	32 193	12	12	Ciidae
Komonen et al. 2004	**12**	FIN	LR	1864	1	*Fpin*	45658	<273	12	
Jonsson et al. 2001	**12**	SWE	LR	770	1	*Ffom*		12	12	*Bret, Ohae*
Jonsson & Nordlander 2006	**11**	SWE	FX	240	1	*Fpin*		11	11	
Jonsson et al. 1997	**10**	SWE	FX		2	*Fpin, Ffom*		5	5	*Dorcatoma, Cis, Bret*
Komonen 2003c	**9**	FIN	LR	180	1	*Fpin*	3054	9	9	*Cgla, Cqua*
Orledge et al. 2009	**9**	NEur	Mus, FC		9*	*genera		1	1	*Cbil*
Semenov 2008	**8**	RUS	FC		2	*Ffom, Fpin*		125	4	Aleochar-inae
Süda & Nagirniy 2002	**6**	EST	LR					7	6	*Dorcatoma*
Paviour-Smith 1964	**5**	GBR	FC, LR		5			1	1	*Tfun*
Rukke 2002	**5**	NOR	LR	587	1	*Ffom*	8000+	5	5	Ciidae, *Dorcatoma*
Komonen et al. 2003	**5**	FIN, CHN	LR	297	2(3)	*Fpin, Fros*		5	5	Ciidae, *Dorcatoma*
Jonsell 1998	**4**	SWE			4	*Ffom, Irad, Irhe, Iobl*				*Dorcatoma*
Komonen et al. 2001	**4**	FIN	LR	968	2	*Fros, Alap*	2806	73	2	*Hallomenus, Cden*

				Polypores			Beetles			
Study	**Mx**	**C**	**Md**	**N**	**Nsp**	**Key taxa**	**N**	**Nsp**	**NPsp**	**Key taxa**
Komonen 2008	**4**	FIN	FC, FX	24	1	*Toch*	257	4	4	Ciidae
Kaila et al. 1994	**3**	FIN, RUS	TR	36	3	*Ffom, Fpin, Pnig*	15957	158	~25	
Jonsson et al. 2003a	**2**	SWE, DEU	FC, LX		1	*Ffom*		2	2	*Bret, Ohae*
Jonsell & Nordlander 1995	**2**	SWE	FX, LX	72	2	*Fpin, Ffom*		96		
Komonen 2001	**2**	FIN	LR	928	2	*Fros, Alap*	2020	72		
Jonsell & Weslien 2003	**2**	SWE	FC	54	2	*Fpin, Gsep*	499	49	~10	
Jonsell et al. 2005	**2**	SWE	FC	20	2	*Fpin, Tabi*	803	42	~20	
Jonsson 2003	**2**	SWE	FC		1	*Ffom*	419	2	2	*Bret, Ohae*
Guevara et al. 2000c	**2**	GBR	FC, LX	20	1	*Tver*		2	2	*Cbol, Ogla*
Jonsson et al. 2003b	**2**	SWE	Mod		1	*Fpin*		2	2	*Dpun, Cqua*
Guevara et al. 2000a	**2**	GBR	FX	207	1	*Tver*		2	2	*Cbol, Ogla*
Paviour-Smith 1960b	**1**	GBR	Mus					1	1	*Cbil*
Paviour-Smith 1963	**1**	GBR	FC		1	*Pbet*		1	1	*Tfun*
Paviour-Smith 1965	**1**	GBR	FC, LR		1	*Pbet*		1	1	*Tfun*
Paviour-Smith 1966	**1**	GBR	FX		1	*Pbet*		1	1	*Tfun*
Paviour-Smith 1968a	**1**	GBR	LX		1	*Pbet*		1	1	*Cbil*
Paviour-Smith 1968b	**1**	GBR	LR	12	1	*Pbet*		1	1	*Cbil*
Sverdrup-Thygeson & Midtgaard 1998	**1**	NOR	LR	900	1	*Ffom*	3000+	1	1	*Bret*
Jonsell 1998	**1**	SWE	LR	811	1	*Ffom*	11	1	1	*Dmin*
Komonen et al. 2000	**1**	FIN	LR	360	1	*Fros*	63	19		
Andersen et al. 2003	**1**	NOR	FC		1	*Pcon*		1	1	*Behn*
Jonsell et al. 2003	**1**	SWE	FC, FX		1	*Ffom*		1	1	*Bret*
Lik 2005	**1**	POL	FC, LR	763	1	*Ffom*	3328	1	1	*Bret*
Knutsen et al. 2000	**1**	NOR	FC, LX	40	1	*Ffom*	1009	1	1	*Bret*
Rukke & Midtgaard 1998	**1**	NOR	FC, LR	587	1	*Ffom*	2153	1	1	*Bret*
Midtgaard et al. 1998	**1**	NOR	FC, LR	1588	1	*Ffom*		1	1	*Bret*
Sörensson 2000	**1**	SWE	FC		1	*Pcon*	56	1	1	*Behn*
Nilsson 1997	**1**	SWE	FX	58	1	*Ffom*	971	1	1	*Bret*
Sörensson 1997	**1**	SWE	FC	1	1	*Pcon*		1	1	*Behn*
Lik & Barczak 2005	**1**	POL	FC	460	1	*Ffom*	15573			*Ciidae*
Orledge & Ewing 2006	**1**	GBR	TR		1	*Pbet*	27	1	1	*Cden*

3. Material and methods

3.1 Study areas

Data on polypore occupancy were collected during six inventories in Lapland, plus one in northern, two in eastern and two in southern Finland. These study sites, listed from north to south, were the Yllästunturi and Aakenustunturi fells and highland in western Finnish Lapland, the Luosto fells in central Finnish Lapland, the Sallatunturi fell area in eastern Finnish Lapland, the Pisavaara Strict Nature Reserve (Rovaniemi commune), the Korouoma Forest Reserve in northeastern Finland (Posio commune), the Koitajoki Natura 2000 site, the Kolvananuuro Nature Reserve and Kirjovaara Forest Reserve, the Kolovesi National Park, and the Repovesi National Park.

In my text Ylläs, Luosto, Salla, Pisavaara and Korouoma are collectively referred as the North (Fig. 1, N), and Koitajoki, Kolvananuuro and Kirjovaara, Kolovesi, and Repovesi are referred as the Southeast (Fig. 1, SE). Supplementary field collections and rearings of beetles were made in various localities in southern Finland (the South in the text: Fig. 1, S) in Etelä-Häme (communes Hämeenlinna, Juupajoki, Lammi, Padasjoki, and Ruovesi), Satakunta (Ikaalinen, Viljakkala), Uusimaa (Helsinki, Karjaa, Kerava, Kirkkonummi, Sipoo, Tammisaari, and Vantaa) and Varsinais-Suomi (Hanko, Naantali, and Turku), and the Åland Islands. All these sites are included in Study V. Study I was carried out in North Karelian Biosphere Reserve (the Koitajoki Natura 2000 site) in eastern Finland, Studies II and III in Finnish Lapland, and Study IV in the Southeast. Since the focus is on old-growth forests, implications to forestry and comparisons across sites with different management histories were intentionally left outside the scope of the thesis.

Studies I–V included in this thesis were conducted in forests where spruce (*Picea abies*), pine (*Pinus sylvestris*), birches (*Betula* spp.), aspen (*Populus tremula*) and goat willow (*Salix caprea*) were the commonest tree species. The studies were located mostly in natural and semi-natural old-growth forests, with the majority of the data collected in nature reserves which are among the least disturbed forest areas in Finland. This ensured high polypore diversity and the presence of fruit bodies at different decomposition stages, enabling collection and rearing of Coleoptera from uncommon and poorly known fungi. Most of the materials were collected in May and August–October, but minor collections were made throughout the year.

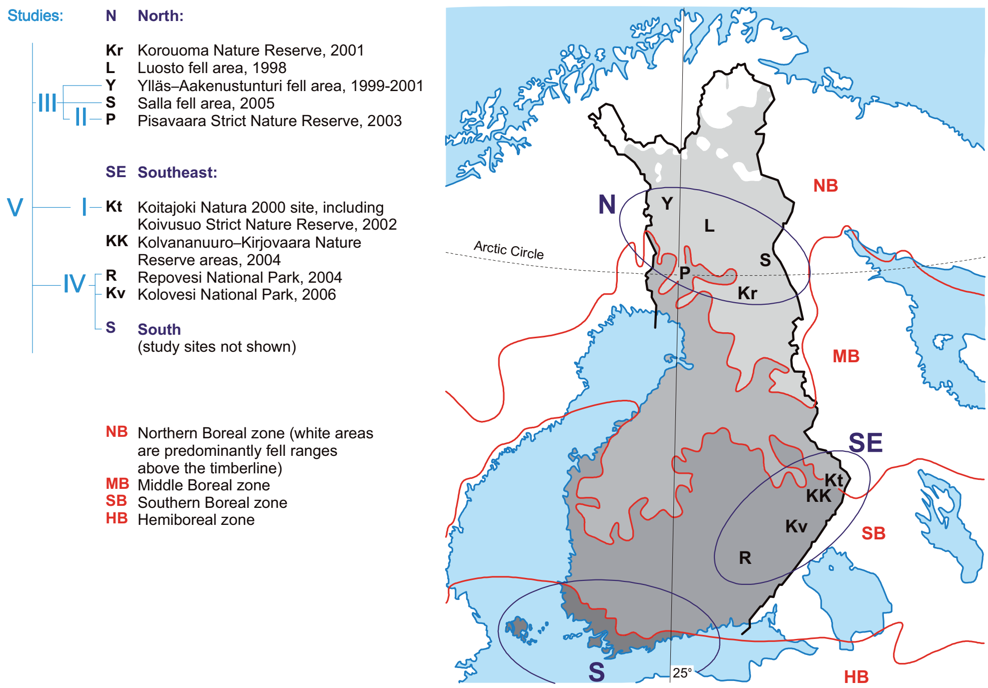

Fig. 1 *Study sites I–V in Finland. Vegetation zones accord Ahti et al. (1968). Study V summarizes the data across Finland.*

3.2 Study system

The main study objects of the present investigation were polypores, i.e. poroid non-bolete Basidiomycetes (Study I–III, V) the majority of which are wood-decaying fungi while a few species are growing on soil. Most species are saprotrophic, but some are pathogens of living trees. There are more than 230 species of polypores in Finland (Niemelä 2005). Epigeal polypores, corticiaceous and hydnoid fungi, and wood-rotting agarics were also collected, the latter specifically discussed in IV. The ecologically close wood-decaying agarics were the primary focus of Study IV, but also touched on in Study I, and together with hydnaceous *Hericium*, in Study III. All studies dealt with fungal fruit bodies, and Studies II and III also with spores. Fungal decay underlying the fruit bodies was not sampled. I explored distribution of polypores in nature reserves in 2001–2007, Study V also includes previous materials from 1998–2001. These eleven polypore inventories were carried out by Tuomo Niemelä and collaborators (University of Helsinki) in Lapland, northern Karelia and Lake District (Fig. 1).

Adult Coleoptera were collected from polypore fruit bodies in the field, while their larvae and pupae were reared into adults in the lab. Species feeding on the interior of the fruit body and species exploiting the surface were the main feeding guilds (Lawrence 1989, Jonsell 1999) of polypore-inhabiting insects in this study.

3.3 Sampling and classification of data

All five studies are based on data collected in the field, with fungi and adult Coleoptera sampled in nature and their larvae reared in outdoor temperature and finally in the lab. In comparison to I–III and V the main difference of Study IV is in the focus on wood-decaying agarics instead of polypores. Trapping, although attractive in its relative neutrality and equality in sampling, was purposely avoided because of missing species-specific information on the catch. This thesis aims to balance the forest biodiversity studies from massive trapping to focus on individual species and delimited communities in accordance with Komonen (2003a). For more details on methods the reader is directed to corresponding sections below and in the individual Studies I–V.

The fungal data

In Studies I and III–V polypore inventories were carried out with uniform methodology, and the presence of polypore species was verified by fruit body observations on living and dead trees, fallen trunks and woody debris in each of the forest compartments (*metsäkuviot*) visited along the roughly pre-planned route. Compartments with the oldest tree stands and the highest amount of dead wood were prioritized, but all forest site types present in the area were searched, mainly spruce- and pine dominated forests, but also small-size targets with supplementary host trees (*Salix*, *Populus* etc., brookside thickets) or forest histories (windthrow, forest fire). Differences in size and shape of compartments were compensated by the time of surveying. Similarly, the size differences among the entire study sites were compensated by the inventory durations. Certain observation errors may have affected the data, as the detectability of polypores depended on the abundance of species within forest compartment (not measured), seasonality of the fruit body (but dead fruit bodies were recorded, when possible to identify), and yearly fluctuations of climate.

Species of polypores were documented; label information of the collected rare and difficult-to-identify species included the host tree, its trunk diameter and decay stage, accompanying fungal species, and the coordinates. Specimens that could not be identified with certainty were collected for microscopic study. These unidentified specimens were dried in ventilated fungus dryers at 40–45° C, and scrutinized with research microscopes, detailed literature, and reference materials. Study II was based on individual collections of *Polyporus pseudobetulinus*. Niemelä (2005) is followed for the fungal nomenclature. These specimens are preserved in the Herbarium of the Botanical Museum of the University of Helsinki (H).

All polypore species were listed for each forest compartment. Forest compartment occupancy was used to measure the prevalence of distribution (Pöyry et al. 2009), i.e. range of polypore species in the protected forests. For each polypore species prevalence was calculated as proportion of the forest compartments occupied by the species out of all the surveyed compartments in an individual study site. Three types of data were treated separately: The variation in prevalence among omnipresent species; the prevalence–

absence data (variation in prevalence among the species present in most study sites); and presence–absence data for species missing from most study sites.

The beetle data

Fungal samples were removed from the substrate and the fruit body surface was carefully examined for living beetles. A fungal sample was an individual fruit body or a cluster of several fruit bodies from, presumably, a single genet. Fruit bodies from soil were always treated individually. As a rule, species of fungi were sampled once per compartment.

The fruit body was then detached, placed to the horizontal 1 m^2 plastic mat and beetles were swept down using a flat brush. If there were few beetles, all fallen individuals were collected by forceps or aspirator into 0.5–1.5 ml collecting tubes. If the beetles were numerous and their moving speed was beyond the author's collecting abilities, everything from the mat surface was directed in a larger container for peaceful sorting in the lab. Such collection routine guaranteed fast and exhaustive sampling of adult beetles. Polypore fruit bodies vary in size and structure among species and individuals, and therefore it is difficult to provide exact timing for every step of the field work. Examination of the sample took from tens of seconds with smallest resupinate species to tens of minutes with large *Grifola* and *Laetiporus*. With the main aim to qualitatively document polypore–beetle species links, accuracy in sample examination and the collecting of all individuals were prioritized over equal sampling effort. On an average, six calendar weeks a year (excluding rearing, see below) were spent collecting with this methodology in 2001–2007.

All polypore fruit bodies examined for adult beetles were also checked in the field for larvae or their traces. Fruit bodies were broken into three or four pieces: colonized fruit bodies break down where the network of larval galleries is densest. The fracture surfaces were visually examined for beetle larvae, which were preserved in 70% alcohol separately from the collected adults. Breaking the fruit body into large pieces and removing the few larvae was carried out in a uniform manner and is unlikely to affect the rearing results. Intact fruit bodies were not collected for rearing, except for the rarest fungal species. The remaining larvae inside the pieces of a colonized fruit body were used for rearing into adulthood in the lab. The following rearing protocol was adjusted according to conditions of a host fungus. Collected pieces of colonized fruit bodies were dried in open plastic bags for 2–3 days in room temperature until their surface became dry. This was an important step to prevent growth of moulds, lethal for beetle larvae. When fruit bodies turned dry on the surface, plastic bags were closed and kept at outdoor temperatures in a sheltered storage for 2–3 months, and then for additional 2–3 months at room temperature. After rearing results were checked and adult beetles preserved for identification, and the remaining larvae, if any, were left for one extra cycle of rearing. Extremely moist and mushroom-like polypores were reared in plastic boxes lined with 1–2 cm of dry gardening peat and closed with fine synthetic mesh. These rearing chambers were stored in outdoor temperature for 2–3 months, moved indoors, where they were moistened by water spray and checked for reared beetles at about two week intervals. From each sample of fungi examined for Coleoptera, all adults collected in the field and all adults reared in the lab were identified and treated separately. Details of methodology and practical advice on collecting and rearing fungivorous Coleoptera are given in a separate paper (Schigel 2008). Silfverberg (2004) is followed for the beetle nomenclature. After completing the mounting, beetles will be donated to the Zoological Museum, Finnish Museum of Natural History, University of Helsinki; single specimens have been given to identifiers (see Acknowledgements).

Under appropriate conditions beetles can reproduce in "wrong" polypore species: Komonen et al. (2001) report over 50 individuals of *C. glabratus* from a single *A. lapponica* fruit body, while the rest of the collected 453 fruit bodies harboured less than ten individuals in total. Taking into consideration large sample sizes needed to distinguish accidental host associations from more stable and ecologically significant associations, in this thesis I aimed to discover and qualitatively document the new fungus–beetle species links. Species whose larvae proved to develop in polypore fruit bodies (breeding records) were selected in accordance with Lawrence (1973: 165) criteria, cited below.

"A breeding record consists of any one of the following: 1) Ten or more fully pigmented adults. 2) Two or more teneral adults. 3) One teneral and two or more fully pigmented adults. 4) One or more larvae and/or pupae (when these can be identified). This breakdown is somewhat arbitrary, but it tends to eliminate accidental records, which are common enough, especially in situations where several very different host fungi… grow on a single log. Cross-contamination in shipment may also account for a certain percentage of accidental occurrences. The added weight given to the presence of teneral individuals is based on the assumption that dispersal flights occur only after full pigmentation (and thus hardening of the cuticle) has been attained. Thus, a teneral adult (if it does not represent a contaminant from an adjacent fruiting body) has almost certainly developed *in situ.*"

Coleoptera were studied in their relation to wood-decaying fungi; in addition a few Diptera and Hymenoptera species were sampled. Collecting and identifying Coleoptera was carried out by the author, except for Ciidae verified by Dr. Alexander V. Kompantsev, Staphylinidae examined by Dr. Viktor B. Semenov, and selected other taxa (mainly of genera *Scaphisoma*, *Dorcatoma*, *Mycetophagus*, *Rhizophagus* and *Epuraea*) scrutinised by Dr. Nikolay B. Nikitsky. Voucher specimens shall be preserved in the Finnish Museum of Natural History.

4. Results

Wood-decaying fungi

During the eleven species inventories in the Finnish North and Southeast, 789 forest compartments were inventoried. A total of 11251 fruit bodies observations out of 153 polypore species were obtained (Study V). In North Karelan Biosphere Reserve (Study I) of the 105 polypore species, 29 were red-listed with different IUCN threat categories, including two endangered species, *Piloporia sajanensis,* and *Antrodia crassa*; 11 vulnerable, and 16 near-threatened (Rassi et al. 2001). These and earlier records sum up to 121 polypore species known by now from North Karelan Biosphere Reserve. In western Finnish Lapland (Study III) 132 polypore species were reported. There were more rare species in the North, including 39 (25.9%) red-listed species. The rarest species in this material were four endangered species, *Antrodia crassa, Polyporus pseudobetulinus* (Study II), *Pycnoporellus alboluteus,* and *Skeletocutis borealis*. Twelve species of polypores were vulnerable and twenty near-threatened. 98 species of polypores were recorded in the survey of 76 forest compartments in Kolovesi National Park (Study IV). These materials were analysed together with results of other inventories in Study V.

Fungicolous Coleoptera

This thesis covers 301 mostly wood-decaying fungi, including 198 species of polypores. Of these 301, 130 (43%) species of fungi were associated with adults or larvae of Coleoptera (Appendix). Out of 198 polypore species, 116 were accepted, and 82 were rejected by Coleoptera. Of the 116 polypore species suitable for adult Coleoptera, 56 were utilized also by larvae. 179 species of Coleoptera were recorded, including 23 species with fungivorous larvae.

In North Karelian Biosphere Reserve 115 polypore-associated beetle species were collected and reared, including 24 species previously unrecorded for the Reserve. In this study site adult beetles or their larvae were found in 52 (49.5%) polypore species, while 53 polypore species appeared uninhabited (Study I). In Lapland 72 fungus-associated species of Coleoptera were collected on 34 (25.8% of studied) polypore species. 34 beetle species reported here are new to the studied area: 15 Coleoptera species were newly collected in the Pallas–Ounastunturi National Park, one is new to Ylläs–Aakenus, and 18 are new to Pisavaara Strict Nature Reserve, including one near-threatened species, *Cis micans* (Study III). In Study II eleven beetles species associated with *Polyporus pseudobetulinus* in Finland and Sweden are reported. Study IV in Kolovesi National Park and southern Finland was focused on beetles living in wood-decaying agarics. 14 species of fungi and 78 species of beetles are reported, including 52 (67%) of Staphylinidae. In Study IV all beetles were sampled as adults, and for *Cychramus* (Figs. 3, 4) and *Triplax* also larvae were recorded. Among solitary agarics, the highest number of beetle species, 13, was collected on *Megacollybia platyphylla*. Of the total 24 beetle species associated with the red-listed polypore *Grifola frondosa* in Ruissalo island, Turku, the most abundant beetle species was *Atheta paracrassicornis* (27% of total individuals sampled from the fungus) and *A. crassicornis* (26%), plus *Lordithon lunulatus* (9%). The less numerous species were mainly Staphylinidae, including eight other species of *Atheta* (Study IV).

In the concluding Study V of 198 species of polypores, a total of 116 species were found to host beetle adults or/and larvae. Altogether 5740 specimens of polypores were examined for Coleoptera in the field. Numbers of polypore samples, those examined for and visited by adult beetles, those collected for rearing beetle larvae into adults, and the numbers of successful rearings are indicated for each polypore species in Study V (Table 2), as are the numbers of beetle species collected in the field or reared in the lab. 82 polypore species were neither visited nor colonized by Coleoptera. A total of 614 fungus–beetle interaction pairs (491 fruit body – adult) were recorded. 1404 polypore specimens were selected for rearing larvae into adults, and disclosed 122 fungus – beetle species interactions pairs (fruit body – larva). The highest number of 47 beetle species was documented for *Laetiporus sulphureus*, followed by *Fomes fomentarius* and *Grifola frondosa*. Altogether 179 species of Coleoptera were documented as associated with polypores in Finland, including 23 (13%) beetle species reared from larvae.

5. Discussion

5.1 Polypore assemblages and prevalence patterns in boreal old-growth forests in Finland

In Study I (Table 4) an attempt was made to describe the species-rich reference areas and compare species composition of polypores in several old-growth forests of Finnish North and Southeast; these ideas were developed with more data in Study V, where differences in polypore prevalence among study sites were discussed. This comparison aimed to outline the polypore species composition in the most valuable undisturbed old-growth forests in Finland, identify the differences in species composition, and find out if prevalence of certain polypore species changes along N–SE gradient. Three groups of species could be identified: northern, southeastern, and omnipresent species.

Study V was based on eleven inventories in northern (Fig. 1N, Studies II, III) and southeastern (Fig. 1SE, Studies I, IV) Finland. These national parks or otherwise protected old forests were uniformly surveyed. Almost 11 200 observations of 153 polypore species occurring in boreal forests allowed to detect the prevailing species. Similar survey was not done in managed forests, but that kind of parallel is likely to reveal differences in the numbers of species and in their order of prevalence. Three types of data comprised the species prevalence – study site matrix: prevalence variations among omnipresent species (31%), prevalence–absence data (46%), and presence–absence data (23%). Each type of data is discussed below, while individual species are treated in Study V.

Twenty-five species of polypores were present in all study sites and demonstrated the narrowest amplitude of prevalence variation across study sites. This group includes all the basic species of any Fennoscandian boreal forest. In the present work carried out in protected forests, the high numbers of threatened or near-threatened (9) species, and those classified as old-growth forest indicators (19 species) are striking. These species would be virtually absent from managed forests. All study sites in my work were old-growth forests. Even though their sizes varied from tens to hundreds of square kilometres, this variation was compensated by the inventory durations.

The prevalent and widely distributed, i.e. the commonest, polypore species such as *Fomes fomentarius*, *Fomitiopsis pinicola*, *Trichaptum abietinum* exhibited stable prevalence ranks across study sites, as did *Inonotus obliquus*, *Antrodia serialis*, *A. xantha*, *Phellinus ferrugineofuscus*, *P. laevigatus*, *P. lundellii*, *P. conchatus*, *Oligoporus sericeomollis*, *T. fuscoviolaceum*, *Gloeoporus dichrous, G. pannocinctus*, *Skeletocutis stellae*, and *Perenniporia subacida*. *Phellinus viticola*, *P. chrysoloma*, *P. nigrolimitatus*, *Gloeophyllum sepiarium*, *Cerrena unicolor*, *Antrodia albobrunnea*, *Amylocystis lapponica*, *Skeletocutis odora*, and *Fomitopsis rosea* showed higher prevalence in the North, whereas *Piptoporus betulinus*, *Phellinus tremulae*, *P. pini*, *Postia caesia*, and *Junghuhnia luteoalba* were more prevalent in the Southeast.

For almost half of the studied polypore species in Study V the prevalence–absence data reflect a northern or southeastern distribution of species. To some extent distributional patterns may be explained by the lack of suitable habitats in certain areas. However, all the study sites were old-growth, mostly spruce- and pine-dominated forests rich in dead wood.

Despite the differences in wood productivity, fragmentation of old-growth forests, and human history between the North and the East (Kouki et al. 2001), the habitat qualities within old-growth forests may be assumed comparable in these respects. Two polypore groups outlined below may reflect climatic differences between north and south, but also between the northern Atlantic forests, more influenced by the Gulf Stream, and continental taiga (Ahti et al. 1968). Species assemblages of polypores may be determined by the differences in the speed of decay in the trees with different growth rate (Edman et al. 2006) in different climates.

Polypores with a northern prevalence profile were in some cases missing from the Southeast, although almost uniformly present in the North. These include *Onnia leporina*, *Climacocystis borealis*, *Antrodiella pallasii*, *Skeletocutis chrysella*, *Oligoporus parvus, Skeletocutis lilacina*, *Junghuhnia collabens*. In other cases, the northern trend was clear although not so striking (*Cinereomyces lenis*, *Meruliopsis taxicola, Leptoporus mollis, Haploporus odorus*, *Antrodiella parasitica*, *Gloeophyllum protractum, Skeletocutis borealis*, and *Oligoporus balsaminus*). Gradual decrease in prevalence towards the Southeast was observed in *Skeletocutis stellae* and *Trametes velutina*. However, some species known as northern (Kotiranta & Niemelä 1996), e.g. *Trichaptum laricinum, Daedaleopsis septentrionalis, Diplomitoporus crustulinus*, and *Antrodia crassa*, were found also in Koitajoki, an exceptionally diverse and rich site in the Southeast.

Species with higher prevalence in the southeastern sites were *Bjerkandera adusta*, *Inonotus radiatus*, *Trichaptum pargamenum*, *Antrodia macra*, *Phellinus punctatus*. Other species with clear southeastern preference were, e.g. *Rigidoporus corticola*, *Postia alni*, *Oligoporus fragilis*, *Inonotus rheades*, *Datronia mollis*, *Ceriporiopsis pseudogilvescens*, *Trametes hirsuta*, *Antrodia mellita*, and *Phaeolus schweinitzii*. *Spongiporus undosus* and *Lenzites betulinus* were recorded in all southeastern sites, but only in a few northern sites. These findings generally agree with the contrast in polypore assemblages of hemiboreal *vs.* southern *vs.* middle and northern boreal zones discovered by Väisänen et al. (1992) for 43 mostly Hymenochaetaceae polypore species.

Many endangered and vulnerable species, such as *Piloporia sajanensis*, *Pycnoporellus alboluteus*, *Polyporus pseudobetulinus*, *Postia lowei* and *Antrodia primaeva* showed low overall prevalence. Some species were found only in the North, such as *Gelatoporia subvermispora* (Ylläs), *Pycnoporellus alboluteus* (Pisavaara), *Antrodiella canadensis* (Salla). *Pycnoporellus fulgens*, *Irpex oreophilus*, *Sarcoporia polyspora, Ceriporiopsis balaenae*, *Diplomitoporus flavescens*, and *Oligoporus floriformis* were observed only in Finnish East and South. *Postia luteocaesia* was discovered as new to Finland in Repovesi in 2004 and in Kolovesi in 2006.

A few species were occasionally recorded in the North and the Southeast, outside their core distribution in the South. In southeastern localities such were *Hyphodontia radula, H. paradoxa*, *Rigidoporus populinus*, *Gloeophyllum odoratum*, *Ceriporia excelsa*, *Junghuhnia nitida*¸ and *Polyporus melanopus*. A few observations of southern polypores were made also in the North, e.g. *Ceriporia purpurea* in Salla, *Daedaleopsis confragosa* in Ylläs, *Antrodiella serpula* in Ylläs and Pisavaara, and *Oligoporus balsameus* in Pisavaara.

Distribution of Finnish Aphyllophorales was analysed by Väisänen et al. (1992) and outlined in the checklist of Kotiranta et al. (2009). Many Finnish polypore species miss detailed distribution maps, the best sources being *Threatened polypores in Finland* by Kotiranta & Niemelä (1996) and individual publications (Niemelä 1972–1985, Niemelä & Kotiranta 1982–1991, Niemelä & Saarenoksa 1989, Renvall 1992). The general knowledge of distributional patterns among polypores has been mainly based on subjective field experience of specialists, and was rarely quantified. This study presents a comparison of polypore prevalences in selected nature reserves in Finland. Groups of northern, southeastern, and omnipresent species of polypores were identified along the N–SE line formed by the study sites.

5.2 Wood-decaying fungi and associated beetles in Finland

This thesis is a qualitative report of polypore and beetle species diversity and interaction patterns in boreal old-growth forests in Finland. Special attention was paid to species of fungi insufficiently explored for associated beetles. Studied fungi totalled 301 mostly wood-decaying species, with polypores accounting for 198 of these. Many of these species are red-listed with different threat categories (Rassi et al. 2001). Of these 301, 130 (43%) species of fungi were associated with adults or larvae of Coleoptera (Appendix). Among 198 polypore species, 116 (59% of studied, or 50% of Finnish) were utilized, and 82 (41%, or 36% of Finnish) species of polypores were rejected by Coleoptera. Of 116 polypore species suitable for adult Coleoptera, 56 (48%) were also grazed by larvae.

179 species of Coleoptera were recorded on 116 species of polypores in this study, including 23 (13%) beetle species with fungivorous larvae in 56 polypore species. Altogether there are at least 200 species of polyporicole Coleoptera in Finland, including about 40 with fungivorous larvae, if beetles of *Fomes*, *Fomitopsis* and *Amylocystis* (excluded from rearing, see Materials and Methods) are included. Based on the Finnish checklist of Coleoptera (Silfverberg 2004) and foreign literature on fungivorous beetles (see Review of literature) the total number of polyporicolous beetles in Finland is expected to reach 250–300 species. Of them, the proportion of beetle species with fungivorous larvae may constitute some 25%, as all doubtful rearing records in this study were treated as records of adult visitors. Thus an estimated 30% of polypore–beetle links in Finland are yet unknown.

In the Moscow region, 261 beetle species, including 87 as larvae, are linked with 61 species of polypores (Nikitsky & Schigel 2004), and in my unpublished data from European Russia, 307 beetle species are associated with 92 polypores. In Study V, I treated 198 Finnish species of polypores with a fungus–beetle interaction matrix comprising 116 polypore *vs.* 179 beetle species (35442 potential polypore–beetle associations, see Mx in Table 1). Only a small fraction of this potential is realized in nature and was documented. Nevertheless, this study seems to be among the first in which real species numbers are covered.

The present work increases the species coverage of a previously fairly unknown microhabitat of which only 7% of Fennoscandian polypore species were studied for beetles in any detail (Komonen 2003a). After this work the coverage of studied polypore species rose to about 60–70%. Data on adults collected on the fruit bodies, and most of the records from resupinate and/or annual polypores are new, and so comparisons are not yet possible. Most of the rearing results agree with earlier studies: for references see Study V. Hanski (1989) points out that fungivores are generally very polyphagous and the number of species dramatically increases with sample size. It is likely that with larger sample size new fungus–beetle species associations will be discovered.

In general, species diversity among polypore-utilizing beetles seems to decrease towards the north. Some 300–400 species of polyporicolous beetles may be expected to be found in European boreal forests. Hemiboreal and nemoral polypores like *Polyporus squamosus* (Klimaszewski & Peck 1987), *Laetiporus sulphureus*, *Fistulina hepatica* and *Meripilus giganteus* (Pers.) P. Karst. alone contribute with tens, if not hundreds, of species of Coleoptera, especially when decomposing. Vulnerable polypore *Grifola frondosa* attracted 24 mostly Staphylinid beetles, with *Atheta paracrassicornis*, *A. crassicornis,* and *Lordithon lunulatus* being the most abundant.

Even though my species interaction matrix of 179 beetles × 116 polypores is one of the broadest reported to date, the consumer/host species ratio is only 1.5. Many beetle species occur or breed in various host fungi, and tens of beetle species were recorded in perennial or large-sized fruit bodies. It is clear that even for a common polypore species a sample size of some tens of fruiting bodies would be needed to observe most beetle species. Species accumulation curves for fungivorous beetles are revealed by Thunes et al. (2000) and Komonen (2003c).

Only a few studies have scrutinized the species-rich assemblages of adult Coleoptera, attracted by polypore fruit bodies (Klimaszewski & Peck 1987, Thunes 1994, Hågvar 1999, Økland 2002), although such fungi serve as secondary habitat alternatives for the opportunistic polyporicolous beetles. The presence and the numbers of Coleoptera species in polypores are directly influenced by the forest characteristics and human activities (Thunes & Midtgaard 1998), and are among the first to react to the changes in habitat quality. Direct collecting from the dead wood habitats draws a more adequate picture of host-use patterns of saproxylic species (Saint-Germain et al. 2006), and may be recommended as a supplement to trap inventories (Komonen 2003a).

Polypores rejected by Coleoptera

82 (41%) polypore species in my study did not prove to have any imaginal or larval associations to Coleoptera in spite of increasingly thorough search (Studies I, III, V) Epigeal *Coltricia perennis* and *C. cinnamomea* were never grazed or visited when living or dead. Some of the polypores that beetles ignore belong to the genera where beetle associations are known, and still these species were found intact in all cases. Several polypore species unattractive to Coleoptera belong to taxonomically discrete fungal genera, such as *Antrodia* and *Phellinus*. It seems likely that living and dead fruit bodies of certain polypores are unsuitable for Coleoptera at any life stage.

Many species of polypores ignored by Coleoptera were characterised by annual, small, thin, ephemeral and autumnal fruit bodies with erratic fructification, which are found in sheltered, usually moist subcortical sites, e.g. *Anomoporia kamtschatica*, *Byssoporia mollicula*, *Skeletocutis* spp., *Trechispora* spp., and *Ceriporia* spp. Most of the polypores rejected by Coleoptera were found among the least prevalent species. Even though with larger sample size new fungus–beetle links may be discovered for some of the rejected polypores, many of these species were observed in such high numbers that there must be some fundamental reasons for this phenomenon.

Conclusions

Even though the knowledge of fungus–beetle relations continues to grow, quantitative descriptions have by now been possible only for a handful of species of fungi and beetles. Before statistical analyses and experimens can include hundreds of species of fungi and associated beetles known from Nordic countries, their links need to be discovered.

The species coverage in my work was high, but records of individual interspecific associations are low, and therefore statistical analysis of the present data and testing the hypotheses discussed in the Introduction were hardly possible. A more comprehensive collecting of data would improve their suitability for statistical analyses, but problems arise mostly from host rarity and ephemerality. In the selected study system a mosaic-reconstructing approach seemed the only sensible one. However, in addition to new fungus–beetle links reported in this thesis, some aspects of beetle fungivory are speculatively discussed in individual Studies, including structural hypotheses (Studies I and IV), and the temporal factors (Study III). Consistency classes in Studies I and IV, and seasonal types of polypore fruit bodies in Study III were outlined to illustrate the wide range of fruit body characteristics. These terms therefore do not represent a classification resulting from an analysis, but provide a vocabulary to describe patterns in fungus–beetle interactions.

The main value of this study is the substantial new information on polypore prevalence patterns, fungus-beetle interactions, and the high species coverage. At least 50 species of fungi were studied for the associated beetles for the first time. A fairly large group of polypore species is newly reported as neglected by Coleoptera.

- Prevalence patterns of polypores described and compared for eleven boreal old-growth forests in Finland, based on 11251 observations of fruit bodies of 153 polypore species in 789 forest compartments.
- Polypores with a northern prevalence profile were in extreme cases totally absent from the Southeast, although almost uniformly present in the North. These were *Onnia leporina*, *Climacocystis borealis*, *Antrodiella pallasii*, *Skeletocutis chrysella*, *Oligoporus parvus, Skeletocutis lilacina*, and *Junghuhnia collabens*. Species with higher prevalence in the southeastern sites were *Bjerkandera adusta*, *Inonotus radiatus, Trichaptum pargamenum*, *Antrodia macra*, and *Phellinus punctatus*.
- 301 mostly wood-decaying fungi, including 198 species of polypores were studied. Of these 301, 130 (43%) species of fungi were associated with adults or larvae of Coleoptera.
- Of 198 polypore species, 116 were suitable, and 82 were rejected by Coleoptera. 56 polypore species were utilized also by beetle larvae. 179 species of Coleoptera were recorded, including 23 species with fungivorous larvae. The estimated number of polyporicolous beetles in Finland is expected to reach 300 species.

Future prospects

In spite of the good taxonomical knowledge of both fungi and beetles, their interspecific relations, especially concerning threatened species, have been to a large extent unknown. Collecting such data is time-consuming and labour-intensive. In order to expand our knowledge on beetles visiting polypores, it may be recommended to collect beetles from early spring to late autumn at all stages of fruit body growth and decomposition. My overview of fungus–beetle interaction patterns contains many new data and I hope that it might be utilized in testing hypotheses, modelling and making statistical analyses in more focused studies in the future.

Species coverage need to be further improved, and the discovered fungus–beetle interactions need to be studied in depth. A set of deeply focused studies would be needed for an overview of ecological processes and factors which influence fungus–beetle communities (Hanski 1989). A synthesis of factors that influence insect-resource systems (e.g. abiotic *vs.* biotic, competition *vs.* predation/parasitism) would complete the general picture of beetle fungivory.

Stokland (2001) observes that saproxylic biodiversity researchers in Scandinavia tend to treat taxa, such as fungi and beetles, in separate studies, while ecosystem approaches are largely developed in North America. Since then, scientific integration in dead wood research developed e.g. through Nordic Saproxylic Network (Stokland et al. 2006, www.saproxylic.org).

Many aspects of our knowledge of the autecology of fungivorous Coleoptera remained scanty, particularly of the polypore species with annual (=autumnal) fruit bodies. Examination of beetle gut contents, lab choice experiments and culturing the mycelia from beetle faeces may be of particular use in assessing the specificity of fungivorous Coleoptera. Treating fruit body as a single unstructured breeding medium is justified in species diversity and interaction studies. Complex fruiting body structure may enhance species co-existence and thus diversity, and if species occupy different fungal parts, this might enhance coexistence by reducing interspecific competition. Substrate decomposition, consumer succession and other temporal aspects of beetle ecology are among the least studied subjects in this field.

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Appendix

Index of fungi surveyed for associated beetles in Finland. Fungi with beetle records are set in bold face. For details on species biology, threat categories, and numbers of samples and fruit bodies see Studies I–V.

Species	Study
Albatrellus confluens (Alb. & Schwein.: Fr.) Kotl. & Pouzar	III, V
***Albatrellus ovinus* (Schaeff.: Fr.) Kotl. & Pouzar**	III, V
Albatrellus syringae (Parmasto) Pouzar	V
***Amylocystis lapponica* (Romell) Singer**	I, III, V
Amylostereum chailletii (Pers.: Fr.) Boidin	I, III
Anomoloma myceliosum (Peck) Niemelä & K.H. Larsson	V
Anomoporia bombycina (Fr.) Pouzar	I, III, V
Anomoporia kamtschatica (Parmasto) M. Bondartseva	I, III, V
***Antrodia albobrunnea* (Romell) Ryvarden**	I, III, V
Antrodia crassa (P. Karst.) Ryvarden	I, III, V
Antrodia heteromorpha (Fr.: Fr.) Donk	V
***Antrodia infirma* Renvall & Niemelä**	I, III, V
Antrodia macra (Sommerf.) Niemelä	I, III, V
Antrodia mellita Niemelä & Penttilä	I, V
Antrodia primaeva Renvall & Niemelä	I, III, V
***Antrodia pulvinascens* (Pilát) Niemelä**	I, III, V
Antrodia ramentacea (Berk. & Broome) Donk	V
***Antrodia serialis* (Fr.) Donk**	I, III, V
***Antrodia sinuosa* (Fr.) P. Karst.**	I, III, V
Antrodia sitchensis (Baxter) Gilb. & Ryvarden	V
***Antrodia xantha* (Fr.: Fr.) Ryvarden**	I, III, V
***Antrodiella canadensis* (Overh.) Niemelä**	III, V
Antrodiella americana Ryvarden & Gilb.	V
Antrodiella citrinella Niemelä & Ryvarden	III, V
***Antrodiella faginea* Vampola & Pouzar**	I, III, V
Antrodiella pallasii Renvall, Johannesson & Stenlid	III, V
***Antrodiella pallescens* (Pilát) Niemelä & Miettinen**	I, III, V
Antrodiella romellii (Donk) Niemelä	III, V
***Antrodiella serpula* (P. Karst.) Spirin & Niemelä**	III, V
***Armillaria borealis* Marxm. & Korhonen**	IV
Asterodon ferruginosus Pat.	I, III
Bankera fuligineoalba (J. C. Schmidt: Fr.) Pouzar	III
Bankera violascens (Alb. & Schw.: Fr.) Pouz.	III
Basidioradulum radula (Fr.) Nobles	I, III
***Bjerkandera adusta* (Willd.: Fr.) P. Karst.**	I, III, V
***Bjerkandera fumosa* (Pers.: Fr.) P. Karst.**	III, V
Boletopsis grisea (Peck) Bondartsev & Singer	III, V
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk	III
Byssomerulius albostramineus (Torrend) Hjortstam	III
Byssoporia mollicula (Bourdot) Larsen & Zak	I, III, V
Calocera cornea (Batsch.: Fr.) Fr.	I
Cantharellus cibarius Fr.	III
Cantharellus tubaeformis (Bull.: Fr.) Fr.	I, III
Ceraceomyces borealis (Romell) J. Erikss. & Ryvarden	III
Ceraceomyces serpens (Toode: Fr.) Ginns	III
Ceriporia excelsa (S. Lundell) Parmasto	V
***Ceriporia purpurea* (Fr.) Donk**	V
Ceriporia reticulata (H. Hoffm.: Fr.) Domański	III, V

Ceriporia subreticulata Ryvarden	V
Ceriporia viridans (Berk. & Broome) Donk	I, III, V
Ceriporiopsis aneirina (Sommerf.) Domański	III, V
***Ceriporiopsis pseudogilvescens* (Pilát) Niemelä**	I, III, V
***Cerrena unicolor* (Bull.: Fr.) Murrill**	I, III, V
Chaetodermella luna (Romell) Rausch.	I, III
Chondrostereum purpureum (Pers.: Fr.) Pouzar	I, III
Cinereomyces lenis (P. Karst.) Spirin	I, III, V
***Cinereomyces lindbladii* (Berk.) Jülich**	I, III, V
Clavaria purpurea O.F. Müll.: Fr.	III
Clavicorona pyxidata (Pers.: Fr.) Doty	III, V
***Climacocystis borealis* (Fr.) Kotl. & Pouzar**	III, V
Coltricia cinnamomea (Jacq.) Murrill	V
Coltricia perennis (L.: Fr.) Murrill	I, III, V
Columnocystis abietina (Pers.: Fr.) Pouzar	I, III, V
Conferticium ochraceum (Fr.: Fr.) Hallenb.	III
Coniophora olivacea (Pers.: Fr.) P. Karst.	I, III
Coniophora puteana (Schumacher: Fr.) P. Karst.	III
***Crepidotus calolepis* (Fr.) P. Karst.**	IV
Crustoderma dryinum (Berk. & M.A. Curtis) Parmasto	III
Cystostereum murrayi (Berk. & M.A. Curtis) Pouzar	III
Cytidia salicina (Fr.) Burt	I
Daedalea quercina L.: Fr.	V
Daedaleopsis confragosa (Bolton: Fr.) J. Schröt.	III, V
***Daedaleopsis septentrionalis* (P. Karst.) Niemelä**	I, III, V
***Daedaleopsis tricolor* (Bull.: Fr.) Bond. et Sing**	V
Daldinia concentrica (Bolton: Fr.) Ces. & De Not *s.l.*	I
***Datronia mollis* (Sommerf.) Donk**	V
***Dichomitus campestris* (Quél.) Domański & Orlicz**	V
***Dichomitus squalens* (P. Karst.) D.A. Reid**	I, III, V
Diplomitoporus crustulinus (Bres.) Domanski	I, III, V
***Diplomitoporus flavescens* (Bres.) Domański**	V
***Erastia salmonicolor* (Berk. & M.A. Curtis) Niemelä & Kinnunen**	I, V
Fibroporia gossypium (Speg.) Parmasto	V
Fibroporia norrlandica (Berglund & Ryvarden) Niemelä	III, V
***Fistulina hepatica* Schaeff.: Fr.**	V
***Fomes fomentarius* (L.: Fr.) Fr.**	I, III, V
***Fomitopsis pinicola* (Sw.: Fr.) P. Karst.**	I, III, V
***Fomitopsis rosea* (Alb. & Schwein.: Fr.) P. Karst.**	I, III, V
***Funalia trogii* (Berk.) Bondartsev & Singer**	V
***Ganoderma applanatum* (Pers.) Pat.**	I, III, V
***Ganoderma lucidum* (M.A. Curtis: Fr.) P. Karst.**	V
Gelatoporia subvermispora (Pilát) Niemelä	III
Gloeophyllum abietinum (Bull.: Fr.) P. Karst.	V
***Gloeophyllum odoratum* (Wulfen: Fr.) Imazeki**	I, III. V
Gloeophyllum protractum (Fr.) Imazeki	III, V
***Gloeophyllum sepiarium* (Wulfen: Fr.) P. Karst.**	I, III, V
***Gloeoporus dichrous* (Fr.: Fr.) Bres.**	I, III, V
***Gloeoporus pannocinctus* (Romell) J. Erikss.**	I, III, V
Gloiodon strigosus (Schwein.: Fr.) P. Karst.	I, III
***Grifola frondosa* (J. Dicks.: Fr.) Gray**	IV, V
***Hapalopilus aurantiacus* (Rostk.) Bondartsev & Singer**	III, V
***Hapalopilus croceus* (Pers.: Fr.) Bondartsev & Singer**	V
Hapalopilus ochraceolateritius (Bondartsev) Bondartsev & Singer	V
***Hapalopilus rutilans* (Pers.: Fr.) P. Karst.**	I, III, V
***Haploporus odorus* (Sommerf.) Bondartsev & Singer**	III, V
***Hericium cirrhatum* (Pers.) Nikolajeva**	I, III, V
Hericium coralloides (Scop.: Fr.) Pers.	I, III
Heterobasidion annosum (Fr.) Bref.	V

***Heterobasidion parviporum* Niemelä & Korhonen**	I, III, V
Hydnellum aurantiacum (Batsch: Fr.) P. Karst.	I
Hydnellum caeruleum (Hornem.) P. Karst.	III
Hydnellum ferrugineum (Fr.: Fr.) P. Karst.	I
Hydnellum gracilipes (P. Karst.) P. Karst.	I, III
Hydnellum peckii Banker	III
Hydnum repandum L.: Fr.	III
Hydnum rufescens Schaeff.: Fr.	III
***Hygrophoropsis aurantiaca* (Wulfen: Fr.) J. Schröt.**	IV
Hymenochaete fuliginosa (Pers.) Bres.	III
Hymenochaete tabacina (Fr.) Lév.	III
Hyphodontia aspera (Fr.) J. Erikss.	III
Hyphodontia latitans (Bourd. & Galz.) E. Langer	I, V
***Hyphodontia paradoxa* (Schrad.: Fr.) E. Langer & Vesterholt**	V
Hyphodontia radula (Pers.: Fr.) E. Langer & Vesterholt	V
Hypochnicium multiforme (Berk. & Broome) Hjortst.	I
***Hypsizygus ulmarius* (Bull.: Fr.) Redhead**	I, III, IV
Inonotus dryophilus (Berk.) Murr.	V
***Inonotus obliquus* (Pers.: Fr.) Pilát**	I, III, V
***Inonotus radiatus* (Sowerby: Fr.) P. Karst.**	I, III, V
***Inonotus rheades* (Pers.) P. Karst.**	I, III, V
Inonotus ulmicola Corfixen	V
Irpex lacteus (Fr.: Fr.) Fr.	V
Irpex oreophilus (Lindsey & Gilb.) Niemelä	V
***Ischnoderma benzoinum* (Wahlenb.: Fr.) P. Karst.**	I, III, V
Junghuhnia collabens (Fr.) Ryvarden	III, V
Junghuhnia fimbriatella (Peck) Ryvarden	V
Junghuhnia lacera (P. Karst.) Niemelä & Kinnunen	III, V
***Junghuhnia luteoalba* (P. Karst.) Ryvarden**	I, III, V
***Junghuhnia nitida* (Pers.: Fr.) Ryvarden**	V
Kavinia alboviridis (Morgan) Gilb. & Budington	I, III
Kuehneromyces mutabilis (Schaeff.: Fr.) Singer & Smith	III
Laeticorticium roseum (Fr.) Donk	I, III
***Laetiporus sulphureus* (Bull.: Fr.) Murrill**	V
Laurilia sulcata (Burt) Pouzar	III
Laxitextum bicolor (Pers.: Fr.) Lentz	I, III
Lentaria epichnoa (Fr.) Corner	I
***Lentinellus castoreus* (Fr.) Kühner & Maire**	IV
***Lentinellus vulpinus* (Sowerby: Fr.) Kühner & Maire**	I, III, IV
***Lenzites betulinus* (L.: Fr.) Fr.**	I, III, V
***Leptoporus mollis* (Pers.: Fr.) Quél.**	I, III, V
Leucogyrophana romellii (Fr.) Ginns	III
Lycogala flavofuscum (Ehrenb.) Rost	III
***Megacollybia platyphylla* (Pers.: Fr.) Kotl. & Pouzar**	IV
***Meruliopsis taxicola* (Pers.: Fr.) Bondartsev**	I, III, V
Mucronella bresadolae (Quél.) Corner	III
Mucronella flava Corner	III
Mycena tintinabulum Quél.	I
Mycoacia fuscoatra (Fr.: Fr) Donk	I, III
Odonticium romellii (S. Lundell) Parmasto	III
Oligoporus cerifluus (Berk. & M.A. Curtis) Ryvarden & Gilb.	V
***Oligoporus balsameus* (Peck) Gilb. & Ryvarden**	V
Oligoporus balsaminus (Niemelä & Y.C. Dai) Niemelä	III, V
Oligoporus floriformis (Quél.) Gilb. & Ryvarden	V
***Oligoporus fragilis* (Fr.) Gilb. & Ryvarden**	I, III, V
***Oligoporus guttulatus* (Peck) Gilb. & Ryvarden**	I, III, V
Oligoporus hibernicus (Berk. & Broome) Gilb.	I, V
***Oligoporus immitis* (Peck) Niemelä**	V
***Oligoporus lateritius* (Renvall) Ryvarden & Gilb.**	I, III, V

Oligoporus mappa (Overh. & J. Lowe) Gilb. & Ryvarden	V
Oligoporus parvus Renvall	III, V
Oligoporus perdelicatus (Murill) Gilb. & Ryvarden	I, III, V
Oligoporus persicinus (Niemelä & Y.C. Dai) Niemelä	III
Oligoporus ptychogaster (F. Ludw.) Falck	V
Oligoporus rennyi (Berk. & Broome) Donk	I, III, V
Oligoporus romelii (M. Pieri & B. Rivoire)	V
***Oligoporus sericeomollis* (Romell) M. Bondartseva**	I, III, V
***Oligoporus stipticus* (Pers.: Fr.) Gilb. & Ryvarden**	I, III, V
***Onnia leporina* (Fr.) H. Jahn**	III, V
Onnia tomentosa (Fr.) P. Karst.	V
***Panellus serotinus* (Schrad.: Fr.) J.G. Kühn**	I, IV, V
***Perenniporia medulla-panis* (Jacq.: Fr.) Donk**	V
***Perenniporia subacida* (Peck) Donk**	I, III, V
***Phaeolus schweinitzii* (Fr.) Pat.**	I, V
Phanerochaete laevis (Pers.: Fr.) J. Erikss. & Ryvarden	III
Phanerochaete sanguinea (Fr.) Pouzar	I, III
Phanerochaete sanguinea (Fr.) Pouzar	III
Phanerochaete velutina (DC: Fr.) P. Karst.	III
***Phellinus alni* (Bondartsev) Parmasto**	V
***Phellinus chrysoloma* (Fr.) Donk**	I, III, V
***Phellinus conchatus* (Pers.: Fr.) Quél.**	I, III, V
***Phellinus ferrugineofuscus* (P. Karst.) Bourdot**	I, III, V
***Phellinus ferruginosus* (Schrad.: Fr.) Pat.**	V
***Phellinus hippophaeicola* H. Jahn**	V
***Phellinus igniarius* (L.: Fr.) Quél.**	I, III, V
***Phellinus laevigatus* (P. Karst.) Bourdot & Galzin**	I, III, V
***Phellinus lundellii* Niemelä**	I, III, V
***Phellinus nigricans* (Fr.) P. Karst.**	V
Phellinus nigrolimitatus (Romell) Bourdot & Galzin	I, III, V
***Phellinus pini* (Brot.: Fr.) A. Ames**	I, III, V
***Phellinus populicola* Niemelä**	I, III, V
***Phellinus punctatus* (P. Karst.) Pilát**	I, III, V
***Phellinus robustus* (P. Karst.) Bourdot & Galzin**	V
***Phellinus tremulae* (Bondartsev) Bondartsev & Borisov**	I, III, V
Phellinus tuberculosus (Baumg.) Niemelä	V
***Phellinus viticola* (Schwein. ex Fr.) Donk**	I, III, V
Phellodon connatus (Schultz.: Fr.) P. Karst.	III
Phellodon niger (Fr.: Fr.) P. Karst.	I
Phellodon secretus Niemelä & Kinnunen	I, III
Phellodon tomentosus (L.: Fr.) Banker	I, III
Phlebia centrifuga P. Karst.	I, III
Phlebia cornea (Bourd. & Galzin) Parmasto	I, III
Phlebia gigantea Fr.: Fr.	III
Phlebia radiata Fr.	I, III
Phlebia segregata (Bourd. & Galzin) Parmasto	III
Phlebia subulata J. Erikss. & Hjortstam	III
Phlebia tremellosa (Schrad.: Fr.) Burds. & Nakasone	I, III
Phlebiella vaga (Fr.: Fr.) P. Karst. *(P. sulphurea)*	III
Pholiota heteroclita (Fr.: Fr.) Quél.	I
***Pholiota squarrosoides* (Peck) Sacc.**	IV
Phyllotopsis nidulans (Pers.: Fr.) Singer	I, III
Physisporinus vitreus (Pers.: Fr.) P. Karst.	I, III, V
Piloderma fallax (Liberta) Stalpers	III
Piloporia sajanensis (Parmasto) Niemelä	I, V
***Piptoporus betulinus* (Bull.: Fr.) P. Karst.**	I, III, V
***Pleurotus dryinus* (Pers.: Fr.) P. Kumm.**	I, IV
***Pleurotus ostreatus* (Jacq.: Fr.) P. Kumm.**	IV
***Pleurotus pulmonarius* (Fr.) Quél.**	I, III, IV

Plicatura nivea (Sommerf.: Fr.) P. Karst.	I, III
***Polyporus brumalis* (Pers.: Fr.) Fr.**	I, III, V
***Polyporus ciliatus* Fr.: Fr.**	I, III, V
***Polyporus leptocephalus* (Jacq.: Fr.) Fr.**	I, III, V
Polyporus melanopus (Pers.: Fr.) Fr	III, V
***Polyporus pseudobetulinus* (Pilát) Thorn, Kotir. & Niemelä**	II, III, V
***Polyporus squamosus* (Huds.: Fr.) Fr.**	V
Polyporus tubaeformis (P. Karst.) Ryvarden & Gilb.	III, V
Porpomyces mucidus (Pers.: Fr.) Jülich	III, V
***Postia alni* Niemelä & Vampola**	I, III, V
***Postia caesia* (Schrad.: Fr.) P. Karst.**	I, III, V
***Postia lactea* (Fr.) P. Karst.**	V
***Postia leucomallella* (Murrill) Jülich**	I, III, V
***Postia luteocaesia* (A. David) Jülich**	V
***Postia tephroleuca* (Fr.) Jülich**	I, III, V
***Protomerulius caryae* (Schwein.) Ryvarden**	I, III, V
Pseudohydnum gelatinosum (Scop.: Fr.) P. Karst.	I
Pseudomerulius aureus (Fr.) Jülich	I, III
Punctularia strigosozonata (Schw.) Talbot	I
Pycnoporellus alboluteus (Ellis & Everh.) Kotl. & Pouzar	III, V
***Pycnoporellus fulgens* (Fr.) Donk**	I, III, V
***Pycnoporus cinnabarinus* (Jacq.: Fr.) P. Karst.**	I, III, V
Ramaria flava (Schaeff.: Fr.) Quél.	III
***Rhodonia placenta* (Fr.) Niemelä, K.H. Larsson & Schigel**	I, III, V
***Rigidoporus corticola* (Fr.) Pouzar**	I, III, V
Rigidoporus obducens (Pers.: Fr.) Pouzar	V
Rigidoporus populinus (Schumach.: Fr.) Pouzar	III, V
Sarcodon imbricatus (L.: Fr.) P. Karst.	III
Sarcodon squamosus (Schaeff.) Quél.	I
Sarcoporia polyspora P. Karst.	I, V
Serpula himantioides (Fr.: Fr.) P. Karst.	I, III
Sistotrema alboluteum (Bourdot & Galzin) Bondartsev & Singer	III, V
Sistotrema confluens Pers.: Fr.	III
Sistotrema muscicola (Pers.) S. Lundell	III, V
Sistotrema raduloides (P. Karst.) Donk	I, III
Skeletocutis amorpha (Fr.) Kotl. & Pouzar	I, III, V
Skeletocutis biguttulata (Romell) Niemelä	I, III, V
Skeletocutis borealis Niemelä	III, V
Skeletocutis brevispora Niemelä	I, III, V
Skeletocutis carneogrisea A. David	I, III, V
Skeletocutis chrysella Niemelä	III, V
Skeletocutis jelicii Tortić & A. David	III
Skeletocutis kuehneri A. David	I, III, V
Skeletocutis lilacina A. David & Jean Keller	III, V
***Skeletocutis nivea* (Jungh.) Jean Keller**	V
***Skeletocutis odora* (Sacc.) Ginns**	I, III, V
Skeletocutis papyracea A. David	I, III, V
***Skeletocutis stellae* (Pilát) Jean Keller**	I, III, V
***Spongipellis fissilis* (Berk. & M.A. Curtis) Murrill**	V
***Spongipellis spumea* (Sowerby: Fr.) Pat.**	V
Spongiporus undosus (Peck) A. David	I, III, V
Steccherinum ochraceum (Pers.) Gray	I
Stereopsis vitellina (Plowr.) D.A. Reid	I
Stereum hirsutum (Willd.: Fr.) Gray	I, III
Stereum rugosum Pers.: Fr.	I, III
Stereum sanguinolentum (Alb. & Schwein.: Fr.) Fr.	I, III
Stropharia hornemannii (Fr.: Fr.) Lundell	III
Thelephora terrestris Ehrh.: Fr.	I, III
Tomentella bryophila (Pers.) M.J. Larsen	III

***Trametes hirsuta* (Wulfen: Fr.) Pilát**	I, V
***Trametes ochracea* (Pers.) Gilb. & Ryvarden**	I, III, V
***Trametes pubescens* (Schumach.: Fr.) Pilát**	I, III, V
***Trametes suaveolens* (Fr.) Fr.**	V
***Trametes velutina* (Fr.) G. Cunn.**	I, III, V
***Trametes versicolor* (L.: Fr.) Pilát**	V
Trechispora candidissima (Schwein.) Bondartsev	I, V
Trechispora hymenocystis (Berk. & Broome) K.H. Larsson	I, III, V
Trechispora mollusca (Pers.: Fr.) Liberta	I, III, V
***Trichaptum abietinum* (Pers.: Fr.) Ryvarden**	I, III, V
***Trichaptum fuscoviolaceum* (Ehrenb.: Fr.) Ryvarden**	I, III, V
Trichaptum laricinum (P. Karst.) Ryvarden	I, III, V
***Trichaptum pargamenum* (Fr.) G. Cunn.**	I, V
Tubaria confragosa (Fr.) Kühn.	III
***Tyromyces chioneus* (Fr.) P. Karst.**	I, III, V
Vibrissea truncorum Fr.	III
***Volvariella bombycina* (Schaeff.: Fr.) Singer**	**IV**